OVIPOSITION HABITS OF THE TICK DERMACENTOR PARUMAPERTUS NEUMANN AND FACTORS INFLUENCING EGG DEVELOPMENT¹

Clive D. Jorgensen

Of the ticks known to inhabit the desert communities of the Great Basin in western United States, Dermacentor parumapertus Neumann is the most abundant and has the widest geographical distribution (Beck, 1955). Because of its large numbers and wide host and geographical distribution, it is an important tick economically and medically. Diseases known to be harbored by this species in nature are Colorado tick fever and a spotted fever-like rickettsia (Philip and Hughes, 1953; Kohls, 1955), and tularemia (Woodbury and Parker, 1954).

Experimentally D. parumapertus has transmitted Rocky Mountain spotted fever (Mayer, 1911; Parker et al., 1933), and tularemia (Parker. et al., 1937; Allred et al., 1956). Because of its vector po-tentialities, control methods may have to be developed. An understanding of the life history is necessary to develop controlling methods of the tick as well as the diseases harbored and transmitted by it.

Stanford (1934), Cooley (1938), Edmunds (1951), Beck *et al.* (1953), Coffey (1954), Beck (1955), Fremling and Gastfriend (1955), and Gastfriend (1955) have done much to clarify the host relationships, geographical distribution, and bionomics of certain stages in its life cycle, but previous work on the egg stage has been reported in two papers by Hooker *et al.* (1912), and Allred and Roscoe (1956).

The purpose of this study is to furnish more information on the oviposition habits of *D. parumapertus*. The inter-relationships of relative humidity, temperature, percentage of engorgement, pre-oviposition period.² oviposition period,³ post-oviposition period.⁴ oviposition rate, incubation period, host relationships, time of year, and possibly other factors are important concerning the life history of this tick. With the information obtained from this sudy, a better understanding of these phenomena and their influnece on egg development can be had.

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Methods and Materials

Two hundred and fifty black-tailed jack rabbits, Lepus cali-

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²That time lapse between detachment and commencement of oviposition.

³The time during oviposition. ⁴That time lapse between the cessation of oviposition and death.

fornicus deserticola Mearns, collected in Skull Valley, Tooele County, Utah on August 2, 1955 were left at room temperature overnight to allow the engorging ticks to detach. Although most of the ticks did detach, some were removed with eye-muscle forceps. Of the engorged females which detached, a sample of 286 ranging from slight to apparently complete engorgement was selected for this study. Approximately the same number of ticks that were forcibly removed was used for comparative purposes.

Each tick was placed in a two-dram shell vial which was then plugged with gauze-covered cotton and stored in one of five different relative humidity conditions: (1) 100% R.H., (2) 93% R.H., (3) 81% R.H., (4) embedded two inches in moistened verniculite (a commercial insulation material), (5) embedded two inches in moistened sand. All ticks were kept at room temperature which varied from 78° to 86°F. with an average daily mean of 81°F.

The method used for determining the percentage of engorgement was the same as that used by Allred and Roscoe (*op. cit.*). The largest tick collected, weighing 726 7 mgs., was assumed to be 100% engorged and was used as the standard by which the degree of engorgement of other ticks was determined.

The method used by Allred and Roscoe (op. cit.) for the calculation of egg numbers was used in this study. Eight groups of 100 eggs each were weighed and the average weight of an individual egg was determined. This method facilitated the calculation of egg numbers in mass and eliminated the tedious task of counting individual eggs.

To facilitate the handling of eggs, the ticks were divided into weight categories of multiples of 50 mgs. Daily records were kept of the eggs deposited by each tick within each category. The eggs laid each day by all ticks within each category were placed in a separate vial, a new set of vials (one for each category) being used each day. All eggs were kept at a relative humidity of 93% and room temperature.

In order to understand more fully the weight relationships of the engorged ticks and their eggs, each tick was weighed after oviposition was completed and the total weight of the eggs deposited calculated. From these weights and the original weight of the engorged female before oviposition, the loss of weight due to catabolism was determined. This provided a means of determining the efficiency of egg production by each tick.

There natural desert babitats were simulated, i.e. (1) moist sand without vegetative cover. (2) dry sand without vegetative cover, and (3) dry sand covered with debris shed by a greasewood plant. Sarcobatus vermiculatus. All areas were contiguous, and provided with rocks, trunks of bushes, and artificial burrows. Engorged ticks were placed on dry sand and permitted to choose their direction of travel. Data obtained from other studies made by observation of ticks in similar habitats in the field were compared with the laboratory observations

C. D. JORGENSEN

Results

The ticks kept at a relative humidity of 93% required the shortest average pre-oviposition period of 7.8 days. Ticks kept in sand in the laboratory required the longest period of 10.3 days, whereas ticks oviposited in the field within seven days. The average for all ticks which oviposited in the laboratory was 9.3 days (Table 1). No differences were detected between the ticks which were

TABLE 1

Pre-and post-oviposition periods (in days) of *Dermacentor parumapertus*

Holding	Minii	Minimum		Maximum		Average	
Condition	Pre-	Post-	Pre-	Post-	Pre-	Post-	
100% R.H.	7	< 1	25	14	8.9	5.4	
93% R.H.	6	1	18	19	7.8	5.5	
81% R.H.	7	< 1	21	16	9.5	6.0	
Vermiculite	7	1	22	16	9.6	4.6	
Sand	7	1	25	17	10.3	7.0	
Average					9.3	5.7	

pulled off and those that detached themselves. There was no correlation between the length of the pre-oviposition period and the percentage of engorgement.

Sixty-six per cent (188) of the ticks deposited eggs while 34% (98) did not. Thirty-one per cent (30) of the non-ovipositing ticks weighed less than 33.4 mgs., 69% weighed more. Although one tick oviposited when only 4.5% engorged. most were at least 11% to 15% engorged before ovipositing.

The largest tick collected weighed 726.7 mgs. and deposited 6,242 eggs in the laboratory. However, the largest number of eggs (6,563) was deposited by a tick weighing 703.3 mgs. (96.7% engorged). The minimum number of nine eggs was deposited by a tick which weighed 36.3 mgs. (4.9% engorged).

The oviposition period ranged from 3 to 25 days with an average of 15. Fifty-five per cent of the ticks required less than 12 days, while 25% required more than 18 days. There was a very rapid increase in the oviposition period in the ticks from 4.5% to 25% engorgement. As the percentage of engorgement increased beyond 25%, a steady but much less rapid increase in the oviposition period was evident. The relative humidity and temperature conditions under which the ovipositing females were held had no apparent influence on the oviposition period.

Ticks required from 3 to 24 days to complete oviposition, and during the first one-third of the oviposition period, 35% to 60% of the eggs were deposited. During the second one-third of the oviposition period, an average of 30% was laid. An average of 55% of the eggs was deposited by the end of the first one-third of the oviposition period, and an average of 81% by the end of the second one-third.

Ticks from 4.5% engorgement had no peak in their oviposition period. Those of 8:0% to 14% engorgement had a peak on the second day. Those ticks from 15% to 42% engorgement had a peak on the third day, those of 43% to 94% on the fourth day, and those of 95% to 100% on the fifth day. In cases where a peak was evident, it was reached within the first 20% of the oviposition period, after which there was a gradual decrease to completion.

With the exception of 5 ticks which were 25% engorged, the number of eggs deposited was directly proportional to the percentage of engorgement.

Ticks less than 7.0% engorged deposited an average of 0.97 eggs per milligram of total body weight. Those from 7.0% to 34% engorgement averaged 0.19 eggs per milligram of body weight, and those from 34% to 100% averaged 0.12 eggs. The lowest average recorded for any one category was 0.11 eggs per milligram of body weight.

As the percentage of engorgement increased, the percentage of the total weight loss due to egg deposition increased until 90% engorgement was reached, at which time a tendency to level off was noted The percentage of weight loss due to catabolism decreased steadily as the percentage of engorgement increased.

The shortest average post-oviposition period of 4.6 days was demonstrated by ticks in vermiculite, whereas the longest average period of seven days was demonstrated by ticks in sand. An average of 5.7 days was maintained by all of the ticks that oviposited (Table 1). There was no correlation between the post-oviposition period and the percentage of engorgement.

There was no apparent correlation between the percentage of engorgement and the number of days between detachment from the host and death.

Thirteen of the 16 ticks introduced into the simulated natural habitat enclosure burrowed one-half to one inch below the surface of the plant debris to deposit their eggs. Two were accidentally trapped in a hole of the moist sand and one was unaccounted for. All ticks observed in nature crawled into debris where they were later relocated with their respective egg masses.

The egg size ranged from 0.46 mm. to 0.52 mm. in length with an average of 0.47 mm. The transverse diameter ranged from 0.38 mm. to 0.41 mm. and averaged 0.39 mm. No deviations beyond these limitations were observed. Individual eggs averaged 0.08 mg. in weight.

The incubation period ranged from 19 to 35 days, and varied within and between the various humidity conditions. The percentage of engorgement did not influence this period. The time within the oviposition period that the eggs were deposited had no apparent influence on the incubation period.

C. D. JORGENSEN

Discussion and Conclusions

Pre-oviposition Period.— The shortest average pre-oviposition period of 7.8 days was maintained by ticks held at a relative humidity of 93%; the next shortest period of 8.9 days was in 100% R.H. Ticks held at 81% R.H. and in vermiculate averaged 9.5 and 9.6 days, respectively. From ticks collected in July and August, Hooker *et al.* (*op. cit.*) recorded a minimum pre-oviposition period of five and a maximum of six days, but the relative humidity was not reported. This differs from the average of 10 days in 81% R.H. and seven days in 95% R.H. at room temperature as recorded by Allred and Roscoe, (*op. cit.*) who collected their specimens during July. In this study no ticks began oviposition as soon as the five days indicated by Hooker *et al.* Allred and Roscoe observed a decrease in the pre-oviposition period when the relative humidity was increased from 81% to 95%. The ticks in this study followed the same general trend. but an average as low as seven days was never attained.

Even though relative humidity affected the pre-oviposition period, the latter is probably influenced by the temperature as well. Hooker *et al.* recorded the shortest time of five days at 85° F. Although not indicated, the ticks studied by allred and Roscoe were probably kept at an average mean temperature of less than 85% F. as were those of this study. This being the case, temperature can easily be correlated with the length of the pre-oviposition period. Smith (1946) proposed that an increase in the average daily temperature tends to reduce the pre-oviposition period in Dermacentor *variabilis*, but relative humidity has no effect on it. Hixon (1932) pointed out that temperature was a limiting factor in determining the length of the pre-oviposition period of *Ixodes sculptus*. He maintained that the ticks kept at temperatures of 37° and minus 3°C would not deposit eggs until the temperature was changed to 24.5°C. Arthur (1945) indicated that the pre-oviposition period in *Ixodes ricinus* varies with the season, which implies a temperature influence. The effects of temperature on *D. parumapertus* are probably very similar to its influence on these other species.

Vermiculite more closely approaches the natural condition for oviposition than any of the other relative humidity conditions in the laboratory. Consequently ticks in nature may be expected to have an average pre-oviposition period of about 9.6 days though they were observed to begin as soon as seven days.

The effects of temperature and relative humidity do not account for the individual variations among single specimens. Ticks apparently have other limiting factors which may be influenced by the habitat, but not controlled by it. The scope of this study did not include an investigation of these factors although the engorgement period (the time required for the tick to engorge after it has attached) might be suggested as a factor for consideration.

Since engorged females were not collected after they detached freely in nature, it is not known what percentage of engorgement a tick will attain before detaching. Any one of several factors such as the role of the host's blood in simulating detachment, the condition of the host with respect to disease, rapidity of engorgement, food habits of the host, and the de-ticking activities of the host might limit the engorgement period which in turn may influence the preoviposition period.

Percentage of Engorgement and Egg Deposition. — The percentage of engorgement is apparently the factor which determines whether or not the tick will oviposit. Allred and Roscoe (op. cit.) stated that 45 of the 54 ticks that did not deposit eggs weighed less than 60 mgs. In the present study, 30 of 98 non-ovipositing ticks weighed less than 33.4 mgs. (4.5% engorged). which was the lowest limit at which ticks oviposited. Most ticks required at least 11% to 15% engorgement before they began ovipositing. A minimum of nine eggs was deposited by a tick 4.9% (36.3 mgs.) engorged. Allred and Roscoe recorded a minimum of 30 eggs. and reported the smallest tick to lav eggs as being 7.0% engorged. Under natural conditions, ticks probably would not detach voluntarily when only 4.5% engorged, and would therefore be more fully engorged and deposit more eggs. Egg Numbers. — Allred and Roscoe (op. cit.) noted that the largest number of eggs. 6,587, was deposited by a tick weighing slightly less than 515 mgs. They did not indicate the number of eggs produced by their larest tick, which weighed 515 mgs. Hooker et al. (op. cit.) recorded a maximum of 4.660 eggs, but did not indicate the size of the tick ovipositing this number. In the present study. the largest number of eggs, 5,563, was deposited by a tick weighing 703.3 mgs. There is little doubt that fully engorged ticks may deposit more than 6,587 eggs, but the trend was for the maximum number of eggs to remain somewhat constant after this approximate number was reached. Engorged females may reach a point of diminishing returns, at which time a threshold of egg production is reached.

Oviposition Period. — The length of the oviposition period is dependent upon the percentage of the engorgement. Ticks from 4.5% to 25% engorged were extremely variable, ranging from 3 to 16 days, respectively. From 25% to 100%, the rise was much less variable, ranging from 17 to 24 days, respectively. The over-all average of 15 days is very close to the 15.9 days reported by Hooker et al. (op. cit.).

Oriposition Rate. — By dividing the oviposition period into three equal periods of time, differences in the deposition rate of the ticks were noted. The smaller ticks deposited as few as 35% of their eggs during the first one-third of their oviposition period, whereas the larger ticks deposited as much as 60%. All ticks deposited 30% of their eggs during the second one-third. Generally, as the percentage of engorgement increased, there was an increase in the relative percentage of eggs deposited during the first one-third of the oviposition period. Since the percentage during the second one-third remained constant at 30%, the reciprocal of the first one-third was maintained in the final one-third. Since there was no correlation between the relative humidity and percentage of engorgement, it is evident that the rate of oviposition increases independently of the relative humidity as the engorgement more closely approaches 100%.

Ticks at least 7.0% engorged maintained a peak in their oviposition period which was reached at about the first 20% of this time. This probably is constant regardless of the relative humidity. The various conditions to which ticks are subjected probably alter the number of days required to reach the peak in oviposition, but not the percentage of the oviposition period at which the peak is reached. When optimum conditions are known, more work can be done to clarify this point.

Oviposition Efficiency. — Ticks less than 7.0% engorged deposited an average of 0.97 eggs per milligram of body weight, while those from 34% to 100% average only 0.12 eggs. From these data, it may be stated that with an increase in the percentage of engorgement, there is a decrease in the efficiency of the tick to utilize its blood meal. However, this decreased efficiency is not enough to offset the increase in egg potential as the tick continues to engorge. Percentage of Engorgement and Egg Numbers. — A correlation between the percentage of engorgement and number of eggs deposited is evident. Allred and Roscoe (op. cit.) stated that there is a direct correlation between the degree of engorgement and the number of eggs deposited, suggesting no end to the number of eggs possible if the female could continue to engorge This puts the responsibility of limiting the egg number on the elasticity of the tick, or its ability to accommodate large amounts of blood. If a tick weighing less than 515 mgs. laid 6,587 eggs, as reported by Allred and Roscoe. a tick weighing 726.7 mgs should deposit more than 9.400 eggs. Because many ticks weighing 150 mgs, more than the highest egg producing tick did not exceed this figure, it appears that there are other limiting factors. Although many factors may influence this, it may be due to the degree of individual efficency to utilize the blood meal in egg production, as it is governed by enzymatic systems of the individual tick. It has been shown that this degree of efficiency was less among the larger ticks than among the smaller ones. This degree of efficiency among the larger ticks might be an expression of a predetermined number of eggs in the ovaries. It may be concluded that even though the percentage of engorgement influences the egg number, individual differences in efficiency are the limiting factors in the more completely engorged ticks.

Post-Oviposition Period. — A highly variable post-oviposition period was evident within the various relative humidity conditions. Allred and Roscoe (*op. cit.*) indicated a difference of from 1 to 14 days as compared to less than 1 to 19 days found in this study. Because of the wide variance in each of these conditions, it can be concluded that relative humidity is not the controlling factor.

Even though the degree of engorgement influenced the length of the oviposition period, it apparently was not the factor which determined the length of life from detachment to death. This was a combination of the pre-oviposition, oviposition, and post-oviposition period, their inter-relationships, and the inter- and intra-relationships of factors which limit them.

Disposition of Eggs. — Engorged females follow the general pattern of most arthopods by seeking some degree of protection while depositing their eggs. In nature, ticks deposit their eggs in very shallow debris: however, even with this precaution there is a high mortality rate. The eggs are subjected to being washed away by rain, dessicated in dry seasons, and attacked by predators and parasites. However, since the debris is usually under brush, it furnishes the larval ticks with an excellent opportunity to locate their hosts.

Egg Size. — The egg size was about the same as that reported by Allred and Roscoe (*op. cit.*) except in no case were there any abnormally large eggs. The average size for all eggs measured was 0.47 mm, in length and 0.39 mm, in transverse diameter.

Incubation Period. — The factors limiting the incubation period might very well be a combination of the relative humidity as indicated by Allred and Roscoe, (op. cit.) and the accumulated temperature as indicated by Hooker et. al. (op. cit.). Allred and Roscoe recorded an average of 32 days in 95% R.H. and 31 days in 81% R.H., both of which are higher than the 28 days in 93% R.H. recorded in this study. Because the temperatures of Hooker et. al. were higher than those of Allred and Roscoe and those of this study, the average incubation period observed by Hooker et. al. was probably somewhat shorter.

Summary

In this study, 250 jack rabbits. *Lepus californicus deserticola* Mearns, were collected and several hundred ticks of various degrees of engorgement were taken from them. The ticks were distributed in five different conditions of relative humidity: (1) 100% R.H.. (2) 93% R.H.. (3) 81% R.H., (4) moistened vermiculite, and (5) moistened sand. Approximately 400,000 eggs laid by 286 ticks were held at 93% R.H.

The pre-oviposition period ranged from 6 to 25 days with an average of 9.3 days. This period was influenced by the relative humidity and temperature, but the limiting factors lay within each individual tick. The oviposition period, which ranged from 3 to 25 days, was dependent upon the percentage of engorgement. The post-oviposition period ranged from less than 1 to 19 days and was dependent upon a combination of all factors influencing the tick from its detachment to its death.

Ticks began ovipositing when as little as 4.5% engorged, but most of those that oviposited were at least 11% to 15% engorged.

The number of eggs deposited by a single tick ranged from 9 to 6,563. The largest engorged tick recorded weighed 726.7 mgs

The efficiency of the tick in egg production decreased from 0.97 to 0.12 eggs per milligram of total tick weight as the percentage of engorgement increased. The rate of oviposition increased as the

percentage of engorgement increased. Ticks above 7.0% engorgement reached a peak in the oviposition period within the first 20% of the total time. Ticks below 7.0% engorgement had no peak.

There was a definite correlation between the percentage of engorgement and number of eggs deposited by each tick. The number of eggs deposited by individual ticks was influenced by the percentage of engorgement but not controlled by it. Individual efficiency of each tick to utilize its blood meal in egg production was variable, but seemed to be the factor limiting egg numbers in the larger ticks.

Engorged females sought debris, usually under brush, and deposited their eggs less than one inch below the surface. The eggs were about 0.47 mm, in length and about 0.39 mm, in transverse diameter The incubation period ranged from 19 to 35 days and was limited by a combination of the relative humidity and the accumulated temperature.

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